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## Planning for ex situ conservation in the face of uncertainty

### Abstract

Ex situ conservation strategies for threatened species often require long-term commitment and financial investment to achieve management objectives. We present a framework that considers the decision to adopt ex situ management for a target species as the end point of several linked decisions. We used a decision tree to intuitively represent the logical sequence of decision making. The first decision is to identify the specific management actions most likely to achieve the fundamental objectives of the recovery plan, with or without the use of ex-situ populations. Once this decision has been made, one decides whether to establish an ex situ population, accounting for the probability of success in the initial phase of the recovery plan, for example, the probability of successful breeding in captivity. Approaching these decisions in the reverse order (attempting to establish an ex situ population before its purpose is clearly defined) can lead to a poor allocation of resources, because it may restrict the range of available decisions in the second stage. We applied our decision framework to the recovery program for the threatened spotted tree frog (*Litoria spenceri*) of southeastern Australia. Across a range of possible management actions, only those including ex situ management were expected to provide >50% probability of the species' persistence, but these actions cost more than use of in situ alternatives only. The expected benefits of ex situ actions were predicted to be offset by additional uncertainty and stochasticity associated with establishing and maintaining ex situ populations. Naïvely implementing ex situ conservation strategies can lead to inefficient management. Our framework may help managers explicitly evaluate objectives, management options, and the probability of success prior to establishing a captive colony of any given species.

### Disciplines

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# Planning for ex situ conservation in the face of uncertainty

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**Abstract:** *Ex situ conservation strategies for threatened species often require long-term commitment and financial investment to achieve management objectives. We present a framework that considers the decision to adopt ex situ management for a target species as the end point of several linked decisions. We used a decision tree to intuitively represent the logical sequence of decision making. The first decision is to identify the specific management actions most likely to achieve the fundamental objectives of the recovery plan, with or without the use of ex-situ populations. Once this decision has been made, one decides whether to establish an ex situ population, accounting for the probability of success in the initial phase of the recovery plan, for example, the probability of successful breeding in captivity. Approaching these decisions in the reverse order (attempting to establish an ex situ population before its purpose is clearly defined) can lead to a poor allocation of resources, because it may restrict the range of available decisions in the second stage. We applied our decision framework to the recovery program for the threatened spotted tree frog (*Litoria spenceri*) of southeastern Australia. Across a range of possible management actions, only those including ex situ management were expected to provide > 50% probability of the species' persistence, but these actions cost more than use of in situ alternatives only. The expected benefits of ex situ actions were predicted to be offset by additional uncertainty and stochasticity associated with establishing and maintaining ex situ populations. Naïvely implementing ex situ conservation strategies can lead to inefficient management. Our framework may help managers explicitly evaluate objectives, management options, and the probability of success prior to establishing a captive colony of any given species.*

**Keywords:** captive breeding, cost-effectiveness, decision tree, expert elicitation, management, multi-attribute value, reintroduction, zoos

Planear la Conservación Ex Situ de Cara a la Incertidumbre

**Resumen:** *Las estrategias de conservación ex situ para las especies amenazadas generalmente requieren de un compromiso a largo plazo y la inversión financiera para alcanzar objetivos de manejo. Diseñamos un marco de trabajo que considera la decisión de adoptar el manejo ex situ para las especies focales como el punto final de varias decisiones enlazadas. Usamos un árbol de decisiones para representar de manera intuitiva la secuencia lógica de la toma de decisiones. La primera decisión consiste en identificar las acciones de manejo específicas con mayor probabilidad de alcanzar los objetivos fundamentales del plan de recuperación, con o sin el uso de poblaciones ex situ. Una vez que esta decisión ha sido tomada, se decide si se establece o no una población ex situ tomando en cuenta la probabilidad de éxito de la fase inicial del plan de recuperación, como*

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*la probabilidad de la reproducción exitosa en cautiverio. Trabajar con estas decisiones en el orden inverso (intentar establecer una población ex situ antes de que su propósito esté definido claramente) puede derivar en una mala asignación de los recursos, ya que esto puede restringir el rango de decisiones disponibles en la segunda etapa. Aplicamos nuestro marco de trabajo de decisiones en el programa de recuperación de la rana arborícola moteada (Litoria spencer) del sureste de Australia, una especie amenazada. A lo largo de un rango de acciones de manejo posibles, sólo de aquellas que incluyeron el manejo ex situ se esperó que proporcionaran >50 % de probabilidad de de persistencia de la especie, pero estas acciones cuestan más que sólo usar alternativas in situ. Se pronosticó que los beneficios esperados de las acciones ex situ serían compensados con la incertidumbre adicional y los procesos estocásticos asociados con el establecimiento y mantenimiento de las poblaciones ex situ. Implementar ingenuamente estrategias de conservación ex situ puede llevar al manejo ineficiente. Nuestro marco de trabajo puede ayudar a los manejadores a evaluar explícitamente los objetivos, opciones de manejo y la probabilidad de éxito previo al establecimiento de una colonia cautiva de cualquier especie dada.*

**Palabras Clave:** árbol de decisiones, datos de expertos, manejo, reintroducción, rentabilidad, reproducción en cautiverio, valor multi-característico, zoológicos

## Introduction

Ex situ conservation strategies, such as captive breeding for reintroduction and population augmentation, are considered useful tools to help recover threatened species (Bowkett 2009; Conde et al. 2011). However, ex situ (ES) programs have often been criticized for their low success rates and high costs (Wolf et al. 1996; Fischer & Lindenmayer 2000). Additionally, many species that are considered for ES programs may have poor short-term prospects for in-situ conservation, due to continuing threats (as is the case for amphibian species threatened by disease; Zippel et al. 2011). For such species, a long-term ES commitment may be necessary, which is likely to require a substantial financial investment. In these settings, conservation agencies face high-stakes decisions about whether to initiate ES actions for species. These decisions are often complicated by considerable uncertainty and the need to evaluate trade-offs among multiple conservation objectives, such as the desire to conserve multiple species and habitats (Converse et al. 2013b).

In accordance with International Union for Conservation of Nature (IUCN) guidelines (IUCN 2013), we assume that conservation in the wild is the ultimate management objective of ES conservation programs. We do not address other possible roles of ES populations, such as providing individuals for research or to assist fundraising or education to support in-situ conservation. Therefore, the ES programs can be usually characterized by 2 steps: first, establishing an ES population (such as a captive-breeding colony), and second, using individuals in that program to improve persistence of the species in the wild (e.g., by establishing new populations or augmenting existing ones). Management decisions must account for both steps, because their combination determines the ultimate success of a program. In particular, the initial decision—whether to implement ES actions for a target species, hereafter referred to as the “entry” decision—must also consider future actions that will use ex-situ-

generated individuals to support wild populations. In other words, to make defensible decisions, managers must formally consider how ES populations will be integrated with in situ conservation strategies before ES populations are established. Unfortunately, such forethought may be the exception rather than the rule (Snyder et al. 1996).

Decision analysis is the logical structure and ensemble of methods to formally analyze decisions, deal with uncertainty, and account for trade-offs among multiple objectives (Raiffa 1968). ES conservation programs have long been identified as ripe for the application of decision-analytic methods (Maguire 1986; Maguire et al. 1987; McCarthy 1994; Akçakaya et al. 1995). However, the implementation of decision analysis in ES conservation programs has only recently started to gain momentum (Smith et al. 2011; Moore et al. 2012; Converse et al. 2013b; Runge 2013).

In this study, we present a novel decision-analytic framework for the entry decision problem faced by managers considering ES actions for species recovery planning. We use a generalizable decision tree to describe the conditional nature of the 2-step process. Applying the decision tree to an example species, we illustrate how it can be adapted to a specific planning scenario. Our goal in presenting this framework is to provide a logical structure for managers facing the entry-decision problem. Our key argument is that managers should decide whether to implement an ES program by considering a series of linked decisions that account for how the resulting individuals will advance conservation in the wild. Otherwise, managers risk using resources—both money and individuals of the target species—inefficiently.

## Methods

### General Decision Tree for Species-Recovery Decisions

Our framework can be intuitively represented using a decision tree. Decision trees are a graphical representation

of a decision process and can be used to calculate the expected value of alternative decisions in the face of uncertainty (Behn & Vaupel 1982). Although their potential for use in conservation decision making is recognized (Maguire et al. 1987), in practice decision trees remain an underused tool (Rout et al. 2013). In a decision tree, the problem is represented as a flow chart, where paths connecting decision nodes (choices among decision alternatives, conventionally represented as squares) and chance nodes (stochastic processes, represented as circles) lead to discrete outcomes (represented as hexagons). When a specific decision (a branch of a decision node) leads to a stochastic node with a number of possible discrete outcomes, the expected value for that decision is the average value of the outcomes weighted by their probability:

$$EV_a = \sum_{j=1}^J o(a, j) p_j(a), \quad (1)$$

where  $EV_a$  is the expected value of alternative  $a$ . Alternative  $a$  may result in any of  $J$  stochastic outcomes (e.g., persistence or extinction of a population), where each outcome  $j$  given action  $a$  has value  $o(a, j)$  and probability of occurring  $p_j(a)$ . The optimal action then is

$$a^* = \arg \max_a \sum_{j=1}^J o(a, j) p_j(a), \quad (2)$$

where  $\arg \max$  indicates the set of points of the argument for which the function has the maximum value; that is, the optimal action is the one with the maximum expected value (note also  $\sum_{j=1}^J p_j(a) = 1$ ).

Because outcomes reflect management objectives, the values of  $o$  are expressed using relevant units (e.g., number of individuals or monetary costs). Value functions are used to express the relative preferences of decision makers. For example, higher probabilities of persistence can be proportionally more desirable; in which case value might be represented as a nondecreasing exponential function of the actual probability of persistence. Alternatively, if the objective is delisting of the target species and no value is ascribed if the reduced risk is insufficient to delist the species, a step-value function can be used, taking values of 0 or 1 when the conditions for delisting are missed or met, respectively.

The decision tree in Fig. 1 is a generalized scenario for an existing wild population (source) of a target species, the recovery of which may or may not benefit from ES actions. When read from left to right, the decision tree represents the temporal sequence. The first decision is whether to initiate the ES program. At the second tier, there are 2 decisions: choosing the optimal strategy for reintroduction if the ES population is established or choosing how to manage the original population. The decision tree formally illustrates the linked nature of the decisions, in that decisions about managing populations follow the decision to implement ES actions. To solve

a linked decision problem, one begins by solving the second-tier decisions first (“rollback” procedure [Smith 2010]). Intuitively, this means that to decide what to do at the initial decision node (entry), one must have already identified the best management alternatives available at the second-tier decision nodes and the expected value of those optimal alternatives, conditional on the alternatives available at the initial decision node.

In the decision tree, we begin by finding the solutions for the second-tier decision nodes given both the decision to establish an ES program and the decision not to establish an ES program (hereafter, we define these as the ES and no ES branches, respectively). When no ES management is chosen (lower branch in Fig. 1) because no other chance nodes exist in the no ES branch, no further solution is required, and the value of the entire no ES branch is equal to the value of the optimal no ES action available. Given  $J$  possible outcomes for the actions in the no ES branch,  $a^{\text{NE}}$ , this is calculated as

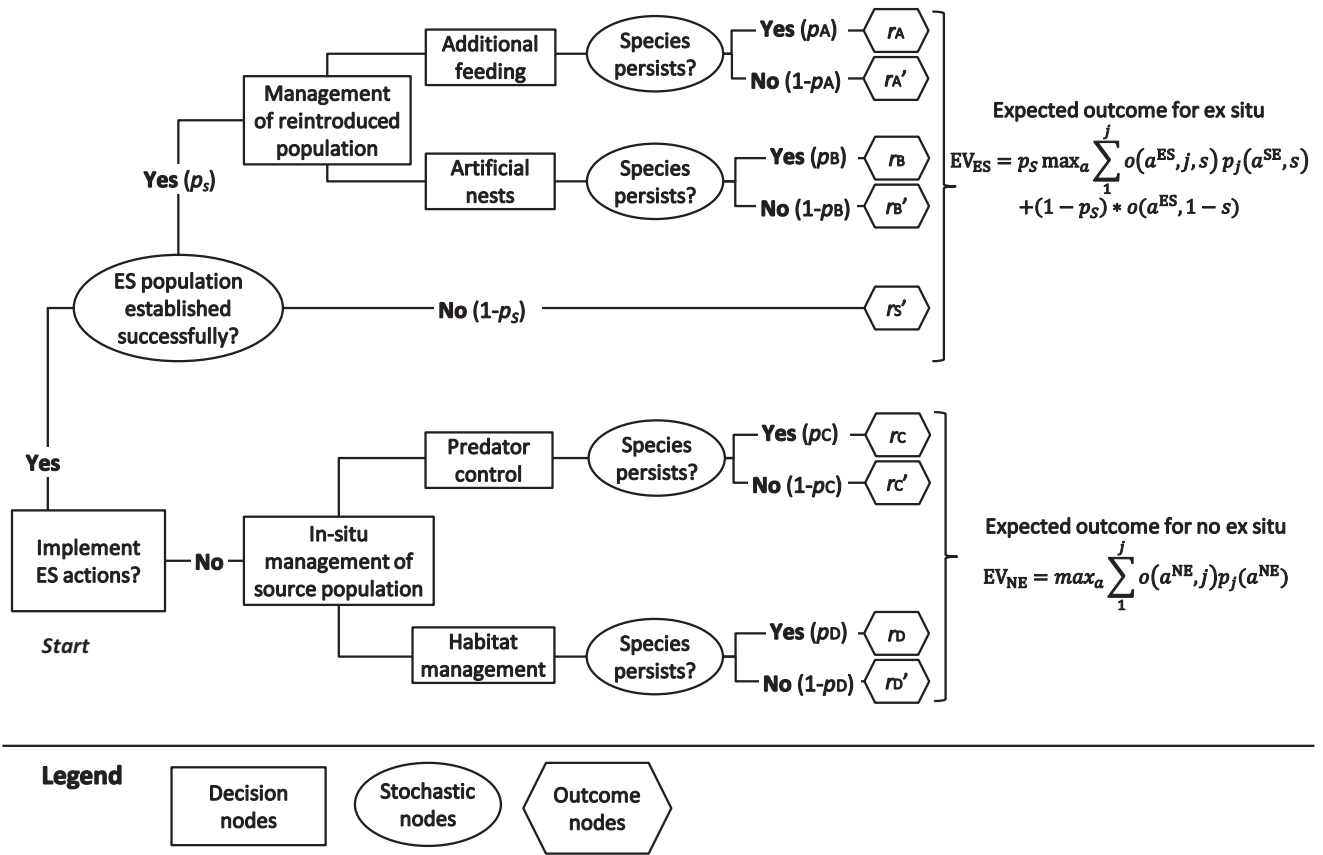
$$EV_{\text{NE}} = \max_a \sum_{j=1}^J o(a^{\text{NE}}, j) p_j(a^{\text{NE}}). \quad (3)$$

Similarly, the first step for the ES branch (upper branch in Fig. 1) is to evaluate the expected outcome of the optimal ES action. However, for this branch, there is an additional source of uncertainty. The optimal reintroduction action can only be carried out if the captive program is established and maintained successfully. Therefore, we worked backward to incorporate the probability of success into the expected outcome. The expected value for the ES branch is calculated as

$$EV_{\text{ES}} = p_s \max_a \sum_{j=1}^J o(a^{\text{ES}}, j, s) p_j(a^{\text{ES}}, s) + (1 - p_s) o(a^{\text{ES}}, 1 - s), \quad (4)$$

where  $s$  represents success in setting up the captive population and  $p_s$  is the corresponding probability of success. Therefore, the first term in the summation represents the outcome of the best action among those that become available if the captive population is established successfully; the second term represents the outcome given failure to establish the ES population. The actual value of the latter depends on the objectives. For example,  $o(a^{\text{ES}}, 1 - s)$  could be zero in terms of persistence, or a negative value if cost, for example, was part of the objective function (because money would have been spent to initiate the unsuccessful captive program). Developing an objective function including multiple objectives (e.g., cost and persistence simultaneously) is dealt with below [and see Eq. (6)].

Thus, the solution to the entry problem is to initiate ES conservation when the expected value of the optimal ES course of action is greater than that of the best of the no ES alternatives considered ( $EV_{\text{ES}} > EV_{\text{NE}}$ ). This direct comparison can usefully be used to analyze the sensitivity of the decision to uncertainty in the parameters. For exam-



**Figure 1.** Decision tree for the choice between implementing or not implementing ex situ actions for a candidate species. After decision nodes (rectangles), labels on arrows indicate the decision alternatives. After chance nodes (circles), labels indicate the possible outcomes of the event (here success or failure). Probability of success is in parentheses. Hexagons represent the rewards for successes or failures (e.g.,  $p_A$  and  $p_{A'}$ , respectively). The equations show the expected outcome of either branch (Eqs. (1)–(3)). Variables are defined in Methods section. We assumed that additional feeding and predator control are the optimal ex situ and no ex situ actions, respectively. For clarity, we show only equations for expected outcomes.

ple, one could determine—given values for  $o(a^{ES}, j, s)$ ;  $p_j(a^{ES}, s)$ ;  $o(a^{NE}, j)$ ; and  $p_j(a^{NE})$ —what values of  $p_s$  will result in  $EV_{ES} > EV_{NE}$ . Where empirical measures of the required parameters for a situation of interest are not available, expert judgment can help develop plausible estimates that most effectively inform decisions (Speirs-Bridge et al. 2010; Martin et al. 2012a). Such methods can prove especially valuable in the management of threatened species, where the need to make urgent decisions leaves little time for the collection of further information (Martin et al. 2012b).

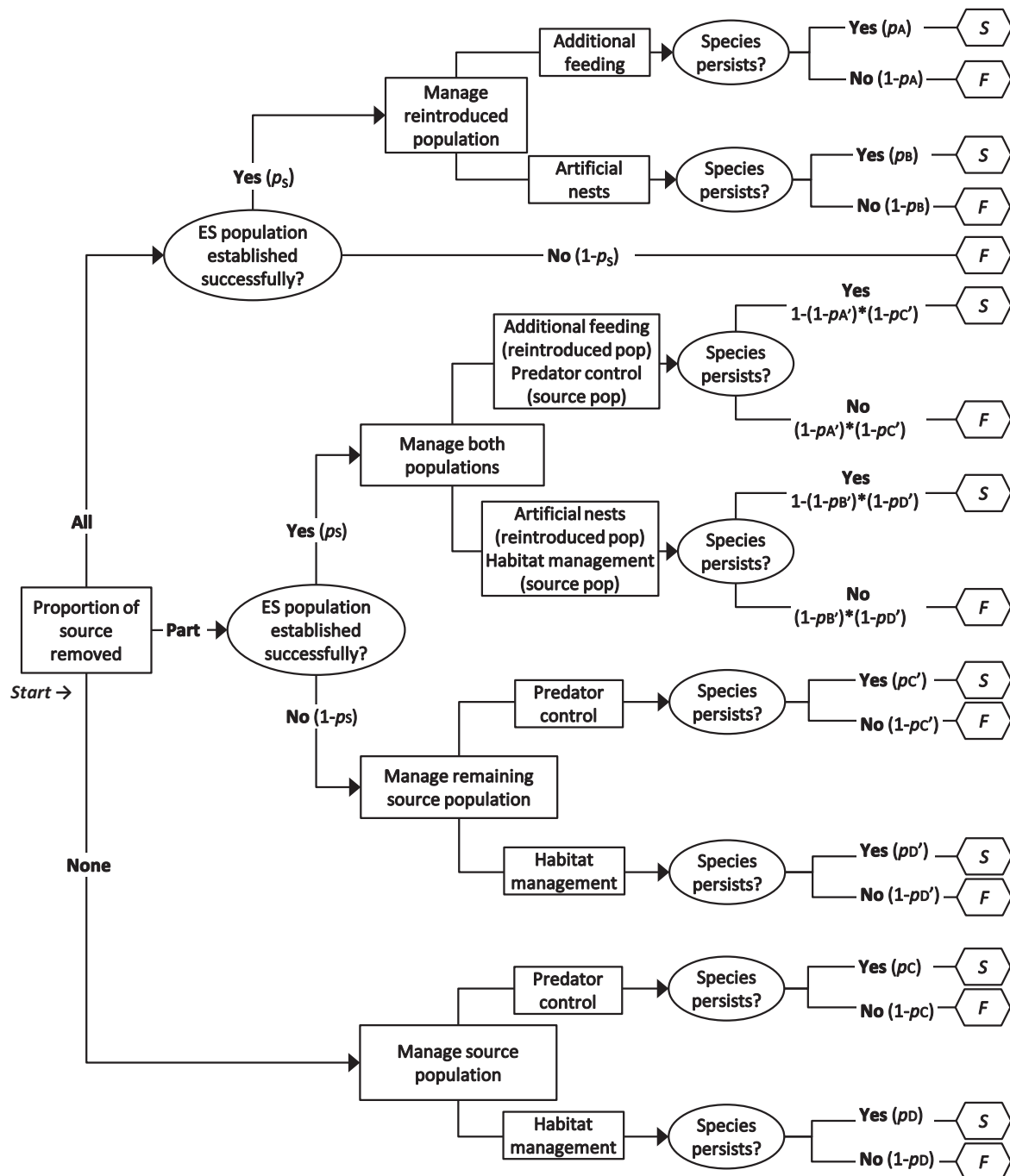
### Ex Situ Management as a Component of Recovery Plans

Normally, ES programs are initiated by removing individuals from the source population. In a mutually exclusive formulation, the ES option would involve removing the entire source population and transferring it to captivity, and the no ES option would be to remove no individuals. However, a realistic program might entail only a

partial removal of the source population. In these circumstances, the smaller remaining source population may be subject to elevated risks arising from demographic and genetic stochasticity (McCarthy 1994; Akçakaya et al. 1995). These risks may offset the benefits of a successful ES program. Managers planning the recovery strategy need to consider the expected benefits of managing an ES population, and eventually a reintroduced or augmented population, and those of managing the remaining source population. In the case of actions that include management of both the source and reintroduced population, the overall expected outcome might be composed of expected outcomes for both populations. One additional possibility is that the ES population is only used to supplement the original source population, resulting in a single population. For the sake of brevity, we do not take up this last possibility in detail here, but in our case study we integrated it into the general framework.

Under the partial-removal scenario, if the ES population fails, it will still be possible to manage the source





**Figure 2.** This figure expands the decision tree in Fig. 1 to account for combined strategies. When only part of the source population is removed, managers have the option of combining management of the reintroduced and source populations. Outcomes change accordingly. We assumed the outcome can be F (for failure, i.e., extinction) or S (for success, i.e., persistence), and the probability of success is the cumulative probability of persistence over both populations. We also assumed that the no ex situ actions for a residual source population are the same, regardless of the ex situ component, but their effectiveness can be modified (e.g., from  $p_C$  to  $p_{C'}$ ) to reflect the influence of attempting an ex situ program regardless of its success.

population. Figure 2 expands Fig. 1 to illustrate two additional scenarios. First, where the ES component succeeds, a new set of actions becomes available in which management can be carried out on both popu-

lations. Second, where the ES population is not established successfully, a set of actions will still be available to manage the remaining source population (these may correspond at least in part to the original no

ES alternatives). Assuming the optimal action will be chosen in each respective set, the expected value of this partial ES strategy can be expressed by modifying Eq. (4) as follows:

$$EV_{(\text{partial ES})} = \sum_{s=1}^S p_s \max_a \sum_{j=1}^J o(a^{\text{partial ES}}, j, s) p_j(a^{\text{partial ES}}, s).$$

The expected values depend on the value functions used. In the simplest scenario, the respective outcomes in the source and reintroduced populations can be considered independent, and value can be realized in both, one, or neither of the 2 populations. For example, if the outcomes  $o$  are measured in units such as the number of individuals, the outcome of a combined strategy, involving management of both reintroduced and source populations, can be calculated as the sum of the respective outcomes (i.e., the sum of both population sizes). If persistence is the outcome of interest, this could be expressed as the cumulative probability of persistence over all existing populations. Alternatively, if the objective is to maximize the number of populations, this can be described by a step function with 3 levels, where  $o = 0$  if both populations fail,  $o = 1$  if a single population persists, and  $o = 2$  if both populations persist.

In a realistic recovery plan, the process of setting up the ES population may change the effectiveness or feasibility of in situ management of the source population. In addition to the aforementioned demographic and genetic impacts of harvesting existing populations, the financial costs of the ES program might need to be covered by diverting resources from in situ management. Synergies can occur; for example, a captive program could leverage additional resources for in situ management or provide new knowledge that improves management of the original population. Scenarios of this type are represented in Fig. 2 with different probabilities of success for management of the source population in the ES branch compared with the no ES branch ( $p'_j$  vs.  $p_j$ ). The ratio of  $p'_j$  to  $p_j$  may be  $>1$  or  $<1$ , depending on the particular situation.

### Case Study

We applied our decision framework to the ongoing recovery of the spotted tree frog (*Litoria spenceri*; Anura: Hylidae). *Litoria spenceri* is endemic to southeastern Australia and is listed as critically endangered by the IUCN (Hero et al. 2004). Severe declines have been observed in the recent past, initially attributed to predation by introduced trout *Salmo trutta* and *Onchorhynchus mykiss* (Gillespie 2001) and habitat degradation (Gillespie 2002). Chytridiomycosis has also been implicated in the species' decline (Gillespie et al. 2014). A recovery plan has been developed with the objective of increasing the abundance of the wild populations to allow a downgrade to a less severe threat category (Gillespie & Clemann 2011).

Proposed actions for in situ management of *L. spenceri* include the removal of invasive weeds and exclusion of introduced trout from sites occupied by extant frog populations. In addition to in situ management, as part of the species recovery plan, a captive breeding program was initiated at two institutions in Melbourne, Australia, in 1990. There are currently approximately 100 adult individuals in captivity, housed in standard facilities (aquaria in quarantined rooms). One institution is successfully producing captive-bred offspring and reintroductions have been carried out regularly since 2005. Survival of reintroduced individuals is currently being assessed by M.W. but appears limited by the presence of chytrid fungus and introduced trout.

While the entry decision for *L. spenceri* has already been made, the recovery plan provides a realistic and convenient test case for our framework. First, the range of possible threats presents managers with a variety of available management strategies, the outcomes of which are uncertain. Second, having already achieved success in establishing an ES population, we can isolate the expected outcomes for the second decision node (the optimal action under both no ES and ES branches) from the probability of success in establishing the ES population, treating the latter as a hypothetical parameter. Therefore, we can make a semiretrospective assessment, simulating the entry decision at the beginning of a recovery effort.

We assumed that the objectives were to maximize the probability of persistence of the species in the wild after 20 years and to minimize management costs. These objectives were aggregated in an additive multiattribute function (Keeney & Raiffa 1993) as

$$EV_{\text{total}(i)} = EV(C)_i w_C + EV(p)_i w_P, \quad (5)$$

where  $EV_i$  is the aggregate expected value of action  $i$ ,  $C$  and  $p$  are the expected cost and probability of persistence, respectively, rescaled to the interval  $[0,1]$ , and  $w_C$  and  $w_P$  are weights between 0 and 1 reflecting the preference for either objective (such that  $w_C = 1 - w_P$ ).

During a dedicated workshop, we asked a panel of 12 experts in amphibian conservation to define a range of possible management strategies for *L. spenceri*. We defined a final set of 32 alternative strategies: one doing nothing strategy 3 involving exclusively in situ management of the existing wild population (combinations of weed control and eradication of introduced trout); and 28 strategies involving the use of ES management for supplementation of existing populations or establishment of new populations. We elicited the probability of persistence and the expected cost under each strategy from the experts. Figures for the expected outcomes are simply indicative values for illustrative purposes. A more rigorous assessment of the recovery plan is currently being undertaken to develop an exhaustive set of alternatives (e.g., the translocation of individuals between extant wild



populations could represent another cost-effective management option).

We assessed the problem retrospectively and investigated how variable weights on persistence of the species and management costs, different value functions, and an imperfect probability of success for the ES component ( $p_s$  in Eq. (3)) would influence the choice of ES or no ES actions. For each possible combination of weights on persistence and cost ( $w_p$  and  $p_s$ , each between 0 and 1), we used the elicited persistence and cost to assign parameters to Eqs. (3)–(4) and used Eq. (5) to calculate the aggregate expected value of all actions. We then solved the decision tree, identified the optimal action under that parameter combination, and determined whether the optimal action involved ES management. We carried out all analyses in R (code in Supporting Information).

In addition to the weights on the objectives, we also considered the possibility that managers could have a nonlinear preference for increases in probability of persistence. For example, managers might be willing to allocate more resources to increasing the probability of persistence from 0 to 0.05 (a minor improvement for a population under extreme threat) than to increasing it from 0.95 to 1 (fully securing a population that is already relatively safe), all other things being equal. We modeled this attitude by repeating the analysis for 3 exponential value functions, defined as

$$EV(p)_i = \frac{1 - e^{\frac{-(p_i - \min p)}{k}}}{1 - e^{\frac{-(\max p - \min p)}{k}}}, \quad (6)$$

where  $p_i$  is the predicted probability of persistence for action  $i$  and  $k$  is an exponential constant used to indicate returns (Kirkwood 1997). We evaluated 3 possible values of  $k$ :  $k = 0.2$  (indicating diminishing returns),  $k = 100$  (a large value used to approximate a linear value function), and  $k = -0.2$  to indicate exponentially increasing values for persistence (as illustrated in Fig. 3b). We assumed that the value function for cost was always linearly decreasing, reflecting a situation in which the cost of a single recovery plan is a relatively minor component of the total budget of an organization (such as a government department).

## Results

On the basis of the elicited outcomes and costs for all possible actions, some ES strategies were expected to result in a greater probability of persistence of *L. spenceri* than no ES alternatives, but this always came at a greater financial cost. For example, the best available no ES strategy (habitat management and eradication of trout) was expected to yield on average a 40% probability of persistence. In comparison, the best available ES strategy (reintroduction of frogs to a chytrid-free site annually for 20 years, habitat recovery, and trout eradication) was

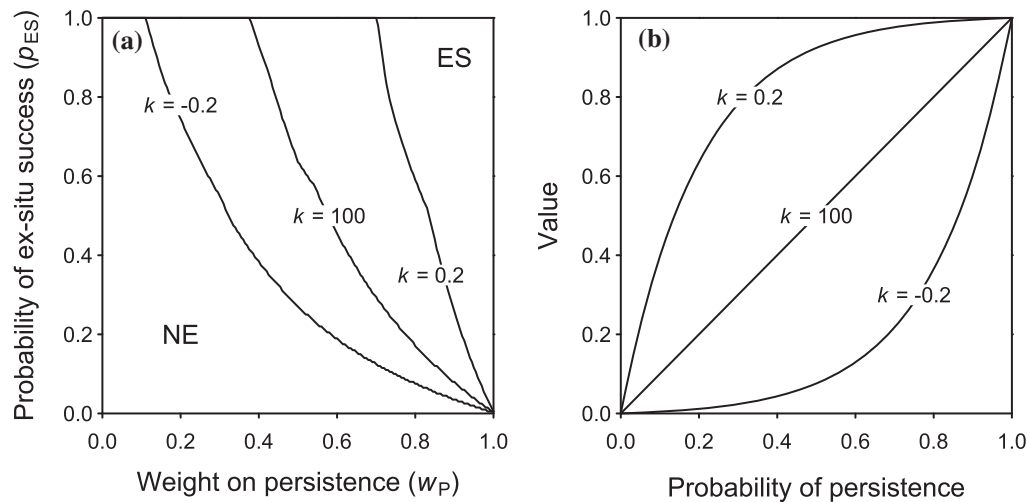
expected to lead to an average probability of persistence of 85%, but the expected cost was almost 3 times greater than the best available no ES action.

When we analyzed different weights in Eq. (5), under the current situation of an ES population of known success ( $p_s = 1$ ), ES strategies were optimal when persistence was considered more important than cost (Fig. 3a). Strategies involving ES actions were also preferred when greater value was placed on high persistence outcomes, as opposed to improvements in the lower part of the persistence range (Fig. 3a). However, when assuming imperfect probability of success in the ES establishment phase ( $p_s < 1$ ), this additional stochasticity offset the greater persistence expected from ES strategies and made them suboptimal. In general, if improving persistence has diminishing value as the species becomes more secure, ES strategies should be avoided except under high values of  $p_s$  and a strong preference for persistence over management costs (Fig. 3a). Conversely, if improvements at high probabilities of persistence do not have diminishing value, ES strategies should be selected (Figs. 3 & 4). Doing nothing was always the preferred action when very strong emphasis was placed on costs (weight on persistence  $w_p < 0.15$ –0.3, depending on the value function used [Fig. 4]), but it would necessarily entail a higher extinction risk.

## Discussion

Reintroduction biology is increasingly embracing decision-analytic methods to improve the management of captive breeding and reintroductions. However, previous studies have mostly focused on decisions about how to use ES programs to achieve recovery in the wild (Smith et al. 2011; Converse et al. 2013a; Runge 2013). To our knowledge, the question of whether to implement ES conservation in the first instance has received little attention (Maguire 1986). However, these two problems cannot be considered in isolation if successful conservation in the wild is the objective. In our simulated retrospective decision, we determined whether bringing *L. spenceri* into captivity would be the optimal decision only after we decided how to use the resulting propagules. The latter decision could only be made once we had compared the expected outcomes of specific management strategies under a given set of objectives.

In the *L. spenceri* case study, with a captive program of known success and individuals available for reintroduction, ES strategies were expected to increase the probability of persistence of the species more effectively than if only the in situ alternative were applied. In the current state, with the ES population already established, the optimal decision was, not surprisingly, to use the captive individuals for reintroduction. However, when we considered the entry problem retrospectively, it was easy to



**Figure 3.** (a) Solution to the decision tree for *Litoria spenceri* across the range of weights for persistence ( $w_P$ ) and all possible probabilities of ex situ conservation success ( $p_S$ ) for each combination of these two parameters: optimal choice is to implement ex situ actions (above the lines) or not to implement ex situ actions (below the lines). No ex situ includes a do-nothing option. In (b), the three solid lines reflect three possible value functions for probability of persistence: a linear relationship (approximated by  $k = 100$ ), diminishing returns (i.e., there is less satisfaction in going from high to very high persistence;  $k = 0.2$ ), and increasing returns (i.e., there is greater preference for very high persistence;  $k = -0.2$ ).

see how different attitudes by decision makers toward the persistence and cost objectives and the possibility of failure in the ES establishment phase might change the optimal decision. For *L. spenceri*, our analysis served only as an example. More robust estimates of such outcomes would be required to make actual management recommendations for this species. However, the factors that influenced the optimal decision in our example are also likely to be relevant for ES programs for other species. Failure to account for such dynamics can lead to suboptimal decisions, misplaced long-term investment of limited resources, and elevated extinction risks for threatened species.

Our case study illustrated how the optimal strategy depended on the values and preferences of managers. Our definition of preferences included a variety of possible factors affecting managers' priorities, from personal moral values to legislation that requires the achievement of specific performance targets. In the *L. spenceri* example, ES strategies incurred a greater cost than alternatives based on in situ actions only, but they were the only options expected to achieve persistence probabilities of 50% or higher. In contrast, strategies that did not involve ES actions were predicted to achieve a lower probability of persistence (<40%), but the estimated financial cost of implementing them was also substantially lower. This is likely to be a common situation for ES programs (Snyder et al. 1996). Decision makers facing this typical conundrum should carefully consider the balance of objectives and the preference for alternative outcomes. Our assessment of different value functions highlighted that ES ac-

tions would be chosen only when placing proportionally greater value on high probability of persistence. ES actions would become less optimal in the case of diminishing returns for higher persistence. It is now generally accepted that reintroductions are unlikely to work unless integrated into a broader recovery plan (IUCN 2013). In support of this, the *L. spenceri* example showed that reintroduction or supplementation was never optimal unless combined with in situ management of the reintroduced population. Our results highlight the real strength of ES programs as components of broad recovery plans aimed at securing species that cannot otherwise be recovered by in situ management alone.

The selection of ES strategies was also driven by the expectations about the establishment of the ES population. Even a moderate probability of failure would have reduced the expected return for choosing strategies involving an ES population. This further highlights the need to consider the sequence of linked decisions, accounting for stochasticity and uncertainty at every step in the decision process. In our case study, we simplified most outcomes as binary (success or failure). For example, we defined success in establishing an ES population as the ability to produce propagules in numbers adequate to carry out a given reintroduction or supplementation action, with a binary outcome (success or failure). We particularly emphasized the importance of failures in the ES phase itself. The definition of ES failure may, of course, differ between specific management actions. Programs that rely on translocation of wild individuals might not require a stochastic node for success of a captive program, but

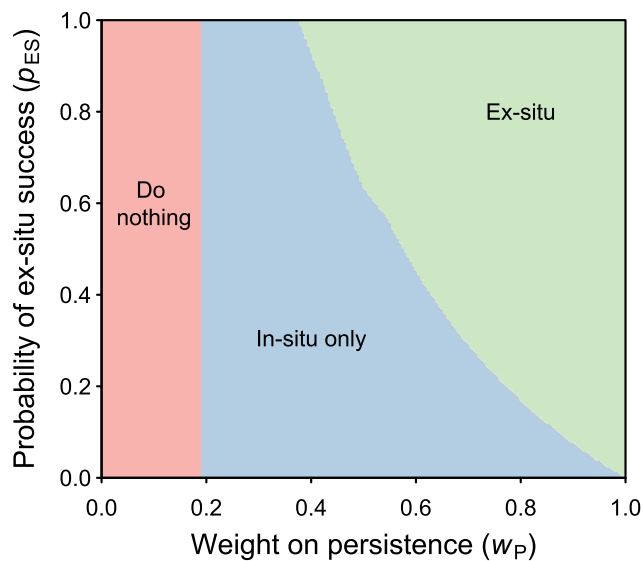


Figure 4. Optimal choice between ex situ, in situ, and do-nothing strategies for *Litoria spenceri*, assuming a linear value function for both persistence and costs ( $k = 100$  in Eq. (6)) and under all possible combinations of objective weights ( $w_p$ ) and probability of successful ex situ establishment ( $p_s$ ).

may introduce a stochastic node to reflect the expected risk to animals during the movement phase (capture and release). At the same time, modified metrics of success might reflect more complex dependencies. For example, the number of individuals released can influence reintroduction success (Sarrazin & Barbault 1996; Green 1997). In this case, success of the ES program could be measured as the number of captive individuals made available for release, influencing the probability of success and the expected outcomes in the release and postrelease phases.

The probabilities of a given outcome (e.g., a given number of individuals available for release) can then be assigned parameters based on the available evidence. Previous studies have highlighted several drivers of success for ES programs, including the size and genetic structure of the founder stock (Earnhardt 1999), available knowledge of ES management, existence of model species, adequate processes for learning (Fischer & Lindenmayer 2000), duration of the ES program (Robert 2009), resources available (Fischer & Lindenmayer 2000), and the captive experience of individuals (Jule et al. 2008). Assessing all relevant knowledge transparently could help identify requirements for additional information. Research and consultations with experts could then focus on areas where additional knowledge is likely to influence the optimal decision. In this sense, ES programs represent ideal candidates for adaptive management approaches (Runge 2013). Our framework provides a sound platform for adaptive management, in which collected data can be

used to update the nodes in the decision tree and the surrounding uncertainty.

The decision of whether to implement ES conservation also implies a decision of when to implement it. In practice, ES management is often delayed until the target species reaches a critical extinction risk, although the delay further diminishes the chances of a successful recovery (Martin et al. 2012b). Funding can also be restricted to highly endangered species, making it difficult to establish ES programs in the early stages of declines. The decision tree can be used to identify the point where the best decision changes to include ES management, for example, a given estimated risk of extinction under the branch with in situ actions only. By monitoring and updating key parameters, managers can determine when to switch from in situ management alone to include ES.

In our example, we assumed the effectiveness of in situ management would not be reduced when the ES program was in place. However, there may be biological and financial trade-offs that may reduce the probability of positive outcomes for the in situ population if an ES population is established. Biological effects may reflect, for example, the removal of individuals from the source population. In financial terms, investing in an ES program can divert resources from in situ efforts. In contrast, ES programs that fund themselves (via exhibits, donations, or other activities) may be independent of resource availability for in situ actions or provide additional benefits. For example, Zoos Victoria's Fighting Extinction program (which involves *L. spenceri*) has provided resources for both ES and in situ actions for threatened species. Captive individuals may also provide additional research opportunities, ultimately improving the effectiveness of in situ actions (Griffiths & Pavajeau 2008). In this case, the implementation of management actions, including in situ management of the existing populations, may become even more effective in the presence of an ES program. Such considerations can easily be incorporated into the decision-making process.

Further conflicts over resource allocation may emerge in a multispecies scheme, where ES management of a given species may involve opportunity costs arising from the inability to dedicate resources to the recovery of another species under a limited budget. Our decision tree can also form the basis for a multispecies prioritization. Recovery plans for multiple species could be compared as part of a decision tree with a broader multiple-objective function that included the probabilities of persistence and management costs for multiple species. A realistic multispecies prioritization should account for the trade-offs, opportunity costs, and synergies between species. Different taxa might benefit, for example, from sharing fixed costs of captive breeding and reintroduction, such as staff time or housing in the same institution. Our decision framework allows a more formal analysis of such management issues.

The main implication of our study is that the decision to bring species into captivity should be made with a long-term view of the broader recovery objectives, rather than as an independent activity outsourced to zoos and managed in isolation from in situ conservation (Redford et al. 2012). Relatively accessible tools, including decision trees, can be useful in analyzing these challenging and high-stake decisions. A rational approach to decision making can promote the efficient use of resources by facilitating constructive collaborations between different researchers and agencies involved in ex situ and in situ management decisions.

## Supporting Information

The R code used to solve the tree for the decision of whether to initiate ex situ conservation for *Litoria spenceri* (Appendix S1) is available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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